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Research

Stress-induced secondary leaves of a boreal deciduous shrub (*Vaccinium myrtillus*) overwinter then regain activity the following growing season

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The ericoid shrub *Vaccinium myrtillus* is one of several deciduous boreal plants that respond to larval defoliation by compensatory production of a new set of leaves within the same growing season soon after defoliation. This new set is termed as 'secondary leaves'. The physiological performance and longevity of secondary leaves is poorly understood. Following a multi-year larval outbreak in boreal Norway, we therefore monitored the fate of the secondary leaves from 2014 to 2016. We observed that secondary leaves were still green upon onset of snow season and that the same leaves were still attached and green when snow melted in spring. During the early growing season of 2015, the overwintering leaves were consumed by moth larvae, but the secondary leaves produced in mid-July 2015 overwintered and were not consumed by larvae the next growing season. Our monitoring shows that most of these leaves remained attached until late August, while the contents of chlorophyll and nitrogen remained high until July. The flavonoid (anthocyanin) content of overwintering leaves increased shortly after snowmelt, and this coincided with a short-lasting colour change from green to violet-bronze. This was probably a protective response to the abrupt increase in solar radiation. Overall, secondary, overwintering leaves were free of snow and physiologically active for ca 6.5 months, which is 2–3 months more than the longevity of primary leaves in the study area. We conclude that wintergreen leaves probably rendered an important carbon sequestration contribution in the critical first phase of the growing season until new side branches with new leaves were developed. Hence, the novel results reported here on the facultative wintergreen growth habit of *V. myrtillus* appears to be a successful strategy.

Keywords: bilberry, compensatory growth, defoliation, facultative wintergreenness, geometrid moths, larval outbreaks, leaf longevity, phenotypic plasticity

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Introduction

Plants can alter their development, physiology, morphology and life history depending on environmental conditions, a phenomenon known as phenotypic plasticity, and this plasticity is often an adaptive response to abiotic or biotic stresses (Schlichting 1986, Mooney et al. 1991, Sultan 2000). Insect herbivory is an example of a biotic stress type that can induce plastic responses in attacked plants, and responses may be defensive to reduce future herbivory or compensatory to regain fitness (Karban and Myers 1989, Agrawal 2001, Kessler and Baldwin 2002). A typical compensatory response is to produce a new set of leaves within the same growing season soon after defoliation, often termed as 'secondary leaves'.

Larval outbreaks of leaf-consuming insects have increased in frequency in northernmost Europe, probably as a result of recent climate change leading to higher winter survival of eggs and more plant biomass during summer (Neuvonen et al. 1999, Jepsen et al. 2008, 2009). Downy birch *Betula pubescens* Ehrh., which dominates over large areas in boreal parts of the Nordic region, is the primary food source for larvae of geometrid moths in this area (Hoogesteger and Karlsson 1992, Jepsen et al. 2009). Larvae also consume much of the forest floor plants under massive outbreaks. Such outbreaks can result in ecosystem shifts, as shoots of ericoid shrubs often die after 2–3 consecutive years of near-complete leaf defoliation, facilitating increased establishment of grasses and bryophytes, which are not consumed by moth larvae (Karlsen et al. 2013, Bokhorst et al. 2015).

The ericoid shrub *Vaccinium myrtillus* L. is a widespread and abundant plant in temperate and boreal forests and heaths, and in alpine heaths (Ritchie 1956, Hultén and Fries 1986), and its leaves are a preferred food source for larvae of geometrid moths. Therefore, this is one of the species that has declined in abundance in larval outbreak areas (Karlsen et al. 2013, Bokhorst et al. 2015). Larval outbreaks may be intense in early summer, but leaf herbivory ceases when caterpillars pupate, which in boreal birch forests normally takes place in early July (Ruohomäki et al. 2000). Phenotypic plasticity is then initiated in birch; it starts to produce secondary leaves from buds of short shoots (Hoogesteger and Karlsson 1992, Heliasz et al. 2011). Similar compensatory plasticity is seen in *V. myrtillus* after simulated rodent herbivory where not only leaves but also shoots were removed (Tolvanen and Laine 1997), and after shoot mortality caused by winter warming stress (Bokhorst et al. 2008, 2011, 2015). However, the post-outbreak plasticity of *V. myrtillus* has, to our knowledge, not been studied in detail.

Here we report on previously unstudied inter-year phenological responses in *V. myrtillus* to larval defoliation. At a monitoring site in an open birch woodland in northern-boreal Norway, we recorded two years of massive larval outbreaks that resulted in near-complete defoliation of both birch and preferred forest floor plants. Similar extensive defoliation was recorded over a large area of northern Norway (Bjerke et al. 2017). *Vaccinium myrtillus* was one of the species that were severely affected by this outbreak. We also observed that a high number of defoliated *V. myrtillus* ramets produced new leaves from around mid-July after the larvae had pupated. We noted that the new leaves were still attached when they became covered in snow in October. We therefore observed the same plants at the time they emerged from the melting snow in the following spring and noted that the leaves had not been shed during winter. We then monitored the longevity and physiology of these overwintering leaves. We here report on these findings showing for the first time that *V. myrtillus* can be facultatively wintergreen as a compensatory (plastic) adaptation to insect defoliation.

Material and methods

Study area

This study was undertaken in Tromsø Municipality (Troms County, north Norway). The main study site was at the small island Håkøya (69.66°N, 18.78°E, 30 m a.s.l.) in a boreal, open low-stature birch (*Betula pubescens*) woodland with understory vegetation dominated by ericoid dwarf shrubs intermixed with mosses and fruticose lichens. A gently sloping west-facing site of ca 50 m^2 was studied over three years (2014–2016). The study site was severely affected by outbreaks of geometrid moths in 2014 and 2015. The caterpillars consumed plant leaves in the first half of the growing seasons. We did not count the density of caterpillars, but applied defoliation rate as an estimate of the plant-relevant severity of the outbreak. The lower birch canopy (0–2 m) suffered from near-complete defoliation in both years, and the outbreak was therefore categorized as extremely severe. When forage resources were depleted in the canopy, the caterpillars continued on the forest floor vegetation, causing a near-complete (> 90%) defoliation of *V. myrtillus* (Bjerke et al. 2017). Other understory plants were also consumed. The outbreaks consisted of largely two species of moth caterpillars, *Epirrita autumnata* and *Operophtera brumata*, and were region-wide, meaning that coastal forests along a stretch of at least 300 km, from Lofoten (68.20°N, 14.34°E) to Karlsøy (70.00°N, 19.83°E), was severely defoliated (Pepi et al. 2017, Bjerke et al. 2017).

A second study site was in an open birch woodland in the west-facing slope of the hill Varden in Tromsø (69.70°N, 18.99°E), 9 km northeast of the Håkøya site. The birch trees and the understory vegetation had similar defoliation rates as the study site at Håkøya. Within an area of 0.22 km^2, the proportion of *V. myrtillus* shoots in different states were estimated shortly after snowmelt in May 2015. The states were shoots without any viable buds (i.e. dead shoots), shoots with viable, swelling buds, and shoots bearing wintergreen leaves. These estimates were made by walking along straight 100-m long lines perpendicular to slope direction and counting shoots when observed.

Measurements at Håkøya

Within the 50 m^2 quadrat, we tagged 11 individual *V. myrtillus* shoots that had been defoliated during summer 2014 but retained compensatory green leaves after senescence had started in autumn (23 September). During the following spring, we collected a leaf from each of those tagged shoots for morphological and physiological measurements. In autumn 2015, we again determined the presence of compensatory green leaves and marked these shoots. During spring 2016, we again measured morphological and physiological characteristics.

From mid-July in 2014 and 2015, within the 50 m^2 site, we observed compensatory leaf production in *V. myrtillus* after caterpillar attacks had ceased. We noticed that compensatory leaves were still attached when the few primary leaves remaining were shed in autumn. In May 2015, shortly after snowmelt, we collected a single leaf from each of 11 shoots. Shoots were selected by a stratified random procedure. From the centre point of the site, cardinal direction and distance in meters were drawn. The plant closest to the drawn position was selected. We repeated this until we had 11 plants. A handheld optical sensor (Dualex Scientific 4, Force-A, Orsay, France) was used to measure the contents of chlorophyll, nitrogen and flavonoids, according to the manufacturer's instructions. Chlorophyll content was later converted to absolute values using the linear equation for dicots in Cerovic et al. (2012). Nitrogen and flavonoids are presented in the manufacturer's units; which for nitrogen is named the 'Nitrogen Balance Index', NBI. The measured area is 5 mm in diameter. We measured on the uppermost leaf if it was large enough to cover the entire measuring area of the sensor. If too small, we selected the next leaf from the top until we found a leaf that was sufficiently large. *Vaccinium* plants in this area are rarely taller than 10 cm, which is typical for this species in low-statured open birch woodland and in alpine regions throughout its distribution range. Thus, lower leaves receive almost the same amount of solar radiation as top leaves.

In addition, in May 2015, we counted the number of wintergreen leaves and alive buds on nine other shoots, selected using the aforementioned random procedure. These shoots were tagged. 23 days later, these tagged plants were resurveyed. Three tags had been removed, possibly by birds. The number of leaves were counted on the 20 plants that we could find. After this, we noticed that many of the wintergreen leaves were consumed during the 2015 larval outbreak, and these tagged shoots were therefore not monitored for the rest of the 2015 growing season.

After the cessation of the 2015 larval outbreak, we again confirmed that compensatory leaves had developed and ascertained that these leaves were still attached upon onset of snow season.

In 2016, the site thawed out in early May. As soon as plants started to emerge from underneath the snow, we once again observed that secondary leaves from the previous season were still attached and green. This time we tagged six randomly selected plants. We were able to monitor the development of these plants from 11 May to 23 August at irregular intervals (from 5 to 26 d between each monitoring). At each day of monitoring, we measured the contents of chlorophyll, flavonoids and nitrogen in three leaves at each plant, as detailed above. The same leaves were measured at each day of monitoring. Selected leaves were also photographed at most visits. New leaves started flushing in mid-May. From 25 May, current-year leaves were large enough to cover the optical field of the instrument, and three new leaves per plant were included in the monitoring. Since all plants of *V. myrtillus* in the area showed clear signs of defoliation, we could not find non-defoliated plants that could serve as controls. Thus, the newly emerging leaves were the closest we could get to a control for comparison with the overwintering leaves.

Colour states of photographed overwintering leaves were in 2016 denoted according to following characters: 1) leaves predominantly green, 2) leaves predominantly violet-bronze, 3) leaves green with few to several yellow-red spots (green area ca 33 to 67 % of total leaf area), and 4) leaves predominantly yellow or pale red (green area less than 33 % of total leaf area). The colour monitoring was applied on the same leaves throughout the growing season. The number of overwintering leaves and number of new side branches per shoot were also monitored at the same occasions.

Statistical analysis

Differences between pairs of data were analysed using Student's t-tests, while time series with multiple data were tested using repeated-measures ANOVA. Relationships between variables were evaluated using linear Pearson correlation coefficients, except for in cases with low n. For these cases, the non-parametric Spearman's rank correlation (denoted as r_s) was applied. Tests were run with SPSS Statistics 24. Data were tested for normality and heterogeneity of variance prior to ANOVAs and correlations.

Data deposition

Data is available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.9ps1n99> (Bjerke et al. 2018).

Results

Vaccinium myrtillus shoots overwintering with leaves were a widespread phenomenon in the study area in 2015 and 2016. A survey in early May 2015 around the hill Varden showed that 32% of shoots bore wintergreen leaves, 59% of shoots were considered dead, and only 9% of shoots were alive with swelling leaf buds and not bearing any wintergreen leaves. Shoots that bore wintergreen leaves were all short and narrow, and leaves were smaller than regular leaf size for this species (Fig. 1a). These shoots had probably developed from rhizomes after the previous growing season's larval outbreak, while dead shoots were generally taller and several years old (Fig. 1b).

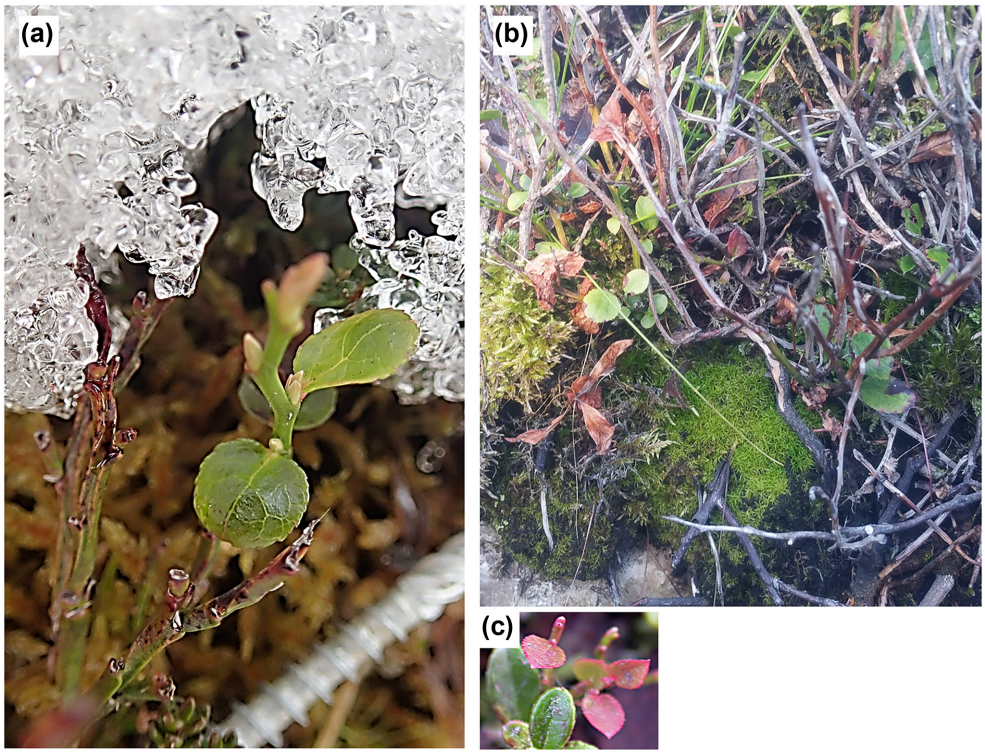

Figure 1. Portfolio of *Vaccinium myrtillus* in various developmental stages. (a) Shoot with wintergreen leaves on the first day in spring without snow cover; the melting snowpack is still surrounding the plant. Later in season, the pale buds developed into new shoot branches with multiple leaves. The shoot to the left had no surviving leaves or buds after larval defoliation. (b) Older and taller shoots of *V. myrtillus* near-completely defoliated by moth larvae, while new leaves are developed on young shoots close to the ground. Photograph from late autumn 2015. (c) Our first documentation of overwintering leaves of *V. myrtillus* (violet-pink leaves). This photograph is from a plot that became snow-free in March 2009 during a simulation of winter warming using infrared heaters, Abisko, northern Sweden; see Bokhorst et al. 2008, 2015 for more information on the experimental design. The dark green leaves on this photograph is *V. vitis-idaea*.

The proportion of shoots with overwintering leaves at our main study site at Håkøya was not estimated in similar detail, but during a survey of the area of ca 50 m^2 in early May 2016, we estimated it to be 35%. Before these observations from 2015 and 2016, we had made one previous observation of this phenomenon; in 2009 we observed two shoots with wintergreen leaves during a winter warming study undertaken in Abisko, northern Sweden (Fig. 1c).

In early May 2015, shoots with wintergreen leaves had on average 11.2 leaves and 6.6 leaf buds shortly after snow thaw (Fig. 2a). The overwintering leaves were on average 5.9 mm long and 4.8 mm wide. These leaves had considerable contents of chlorophyll, nitrogen and flavonoids (Fig. 2b). A survey 23 days later showed that 78% of the overwintering leaves were still attached.

In May 2016, wintergreen shoots at the Håkøya site were monitored from the day they became free of snow. Chlorophyll concentration was 59.5% higher than in overwintering leaves from early May the year before ($t = 3.65$, $p = 0.001$). Average chlorophyll concentrations of overwintering leaves undulated slightly from early May until early July (Fig. 3a). Thereafter, it declined; in late July and late August concentrations were 23.8% and 73.7% lower than maximum (Fig. 3a).

The average chlorophyll content of new leaves was 36% lower than in overwintering leaves at first measurement in late May 2016 ($t = -3{,}40$, $p = 0.004$; Fig. 3a). Chlorophyll concentrations in new leaves increased steadily until early

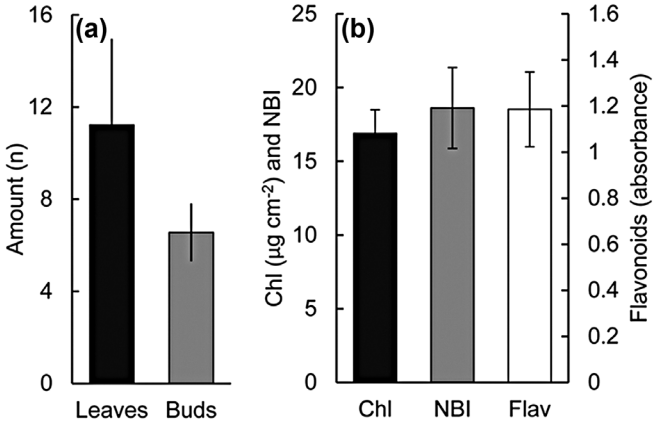

Figure 2. Characteristics of shoots with wintergreen leaves measured ca 5 days after snowmelt in early May 2015. (a) Number of leaves and buds per shoot; (b) contents of chlorophyll (Chl), nitrogen (Nitrogen Balance Index, NBI) and flavonoids (Flav; relative absorbance values). Error bars are ± 1 SEM.

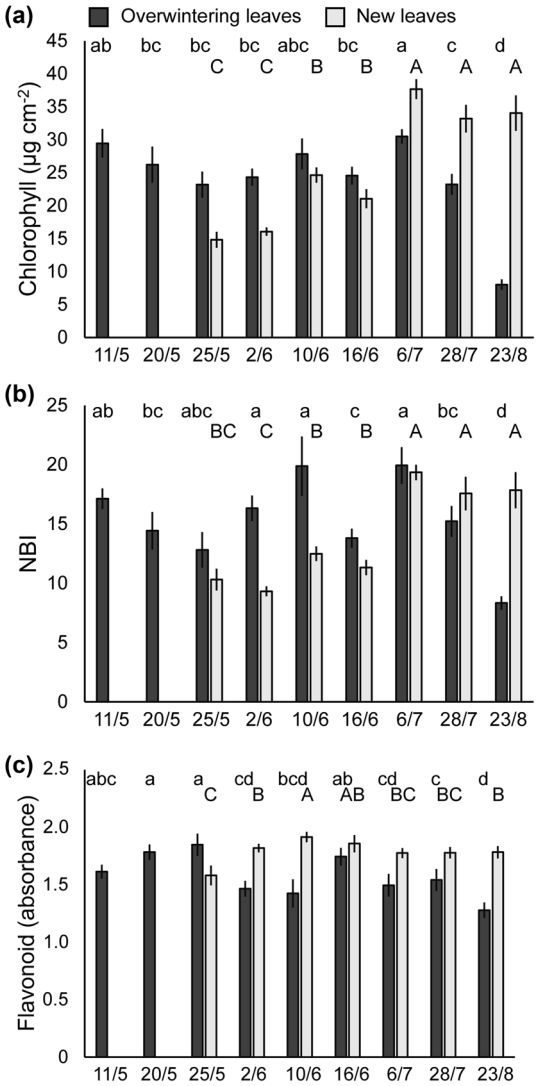

Figure 3. Temporal changes in contents of chlorophyll concentration (a), nitrogen – NBI (b) and flavonoids (c) in wintergreen and new leaves of *Vaccinium myrtillus* from snowmelt in early May 2016 to early autumn in late August 2016. Data points are means of nine leaves (18 at first and last day of measurement). Error bars are ± 1 SEM. Letters placed above bars reflect time differences within the overwintering leaves (lowercase letters) and the new leaves (uppercase letters), respectively. Bars sharing the same letter are not significantly different. New leaves were not large enough to be analysed before 25 May.

July. Thereafter, chlorophyll concentrations remained stable until the last day of measurement in late August (Fig. 3a). Chlorophyll content in new leaves was 42.9% higher in late July ($t=3.59$, $p=0.002$) and nearly 3 times higher in late August ($t=8.11$, $p < 0.001$) than in overwintering leaves (Fig. 3a).

NBI and chlorophyll contents were strongly correlated in both wintergreen ($r=0.785$, $p < 0.001$) and new leaves ($r=0.931$, $p < 0.001$). Hence, the temporal trends in nitrogen content largely follows the same pattern as chlorophyll content, albeit generally with larger variation (Fig. 3b).

Flavonoid content was modestly correlated with chlorophyll in wintergreen leaves ($r=0.350$, $p < 0.001$), but not in new leaves ($r=0.062$, $p=0.630$). Flavonoid content and NBI were weakly inversely correlated (overwintering leaves: $r=-0.255$, $p=0.009$; new leaves: $r=-0.287$, $p=0.023$). During the course of the growing season, flavonoid content of wintergreen leaves varied considerably (with no very clear seasonal pattern), reaching a maximum level in late May (Fig. 3c). Flavonoid content in new leaves was lowest at the first day of measurement in late May and peaked soon after in mid-June before declining only slightly for the rest of the season (Fig. 3c).

Repetitive photographing of single leaves shows some interesting temporal trends, here exemplified by portfolios of two of the studied leaves (Fig. 4). While all leaves were green at the day they emerged from underneath the snowpack in early May, most leaves turned violet-bronze during the first few weeks of exposure (Fig. 4, 5a–d). From 2 June, the violet-bronze colour became less apparent, and leaves were again predominantly green (Fig. 5e–f). This early-season colour change coincided with changes in chlorophyll concentration ($r_s=0.894$, $p=0.041$; five points in time with data on both leaf colour and chlorophyll), while flavonoid absorbance peaked at 25 May (Fig. 3c), viz. the same day as leaves were most distinctly violet-bronze (Fig. 5d). By summer solstice, leaves were still green, but had many red spots (Fig. 5g), and this was also the prominent state in late July (Fig. 5h). By late August, the overwintering leaves had become predominantly yellow-red (Fig. 5i), while current-year leaves still were

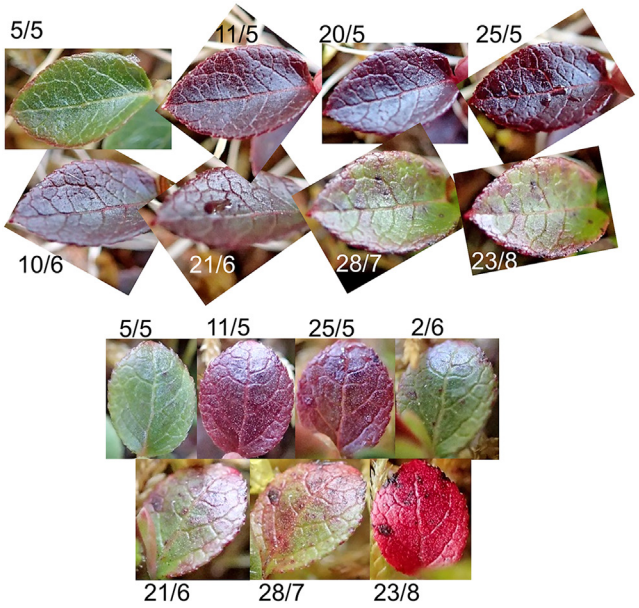

Figure 4. Photographic documentation of changes in leaf colour of overwintering leaves. Uppermost panel shows a top leaf, while the lowermost panel shows a side leaf on another shoot; this leaf quickly became shaded by the developing side branches.

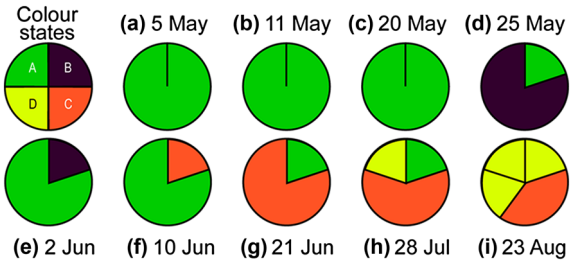

Figure 5. Temporal changes in frequency of leaf colour state during the 2016 growing season. The colour states are: (A) green, (B) violet-bronze, (C) green with few to several yellow-red spots, (D) yellow to pale red. See text for further information on leaf colour states. Values are means of leaves from five separate shoots. Two of the leaves are shown in Fig. 4.

predominantly green (data not shown). For the growing season as a whole, the frequency of overwintering leaves in the green state was strongly correlated with chlorophyll concentrations ($r = 0.776$, $p = 0.040$).

By late August 53% of the wintergreen leaves were still attached (Fig. 6a). Side branches started to develop in late May, and no new side branches emerged after 10 June (Fig. 6b). Instead, side branches expanded multiple times and produced several new leaves, but this was not monitored in detail.

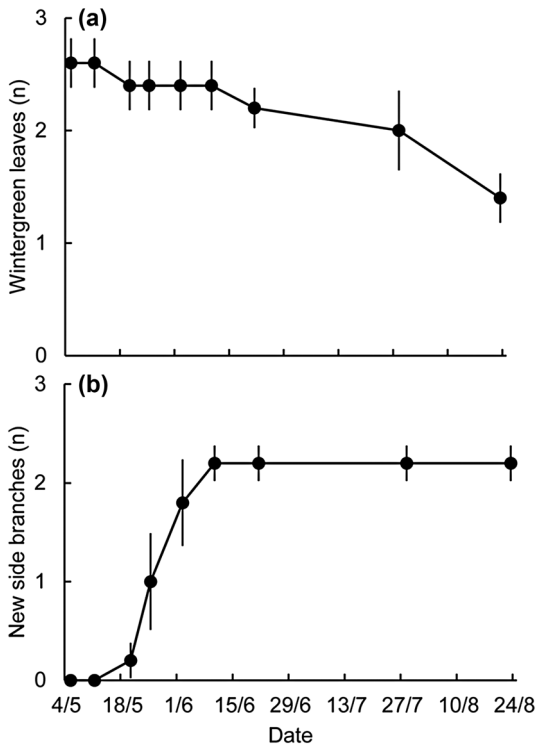

Figure 6. Number of remaining wintergreen leaves per shoot (a), and number of new side branches per shoot (b) from snowmelt in early May to early autumn in late August 2016. Data points are means of five shoots. Error bars are ± 1 SEM.

Discussion

Facultative, or occasional, wintergreenness is known from a series of polar semi-desert plants, for example in species of *Draba* and *Papaver* (Bell and Bliss 1977), some continental Apiaceae species (Petrova 2015), and several temperate macrophytes (Wiegleb et al. 2014). While the polar semi-desert plants in some years have leaves that survive into the next growing season (Bell and Bliss 1977), the wintergreen leaves of the Apiaceae species are shed in late winter before flushing of new leaves (Petrova 2015). Facultative evergreenness is a related process and is known from plants from warmer biomes, for example the North American steppe plant *Atriplex canescens* (Petersen et al. 1987) and the east-Asian submerged water plant *Isoetes sinensis* (Kang et al. 2005).

However, facultative wintergreenness in boreal plants is an understudied plastic response. It is previously known that basal leaves on low-sheltered shoots of *V. myrtillus* may overwinter (Grime et al. 1988), but to our knowledge, the longevity and physiological activity of these leaves in the next growing season has not been analysed previously. Our results suggest that the facultative wintergreen growth habit of *V. myrtillus* is a successful strategy, as the wintergreen leaves remained physiologically active for most of their second growing season. Overall, over the two growing seasons, the leaves were active and free of snow in ca 6.5 months (from mid-July to late September in the first year and from early May to late August in the second year), which is longer than the normal leaf span of *V. myrtillus* in the study area; a primary leaf is normally active for ca 3–4 months, depending on onset of spring and first frost in autumn.

The rapid colour change after emergence from snow, which coincided with a decline in chlorophyll concentration, could easily be interpreted as a senescence process. However, as the image portfolios show (Fig. 4), leaves became violet-bronze-coloured and not yellow-red, which is the more common autumn coloration. The colour change in early growing season was also associated with an increase in flavonoids, and we interpret the violet-bronze colours as an anthocyanin accumulation. Anthocyanins are a group of flavonoids, and *V. myrtillus* leaves produce a number of anthocyanins; Martz et al. (2010) monitored seasonal change in anthocyanin content of *V. myrtillus* in Finland, but did not incorporate the period shortly after snowmelt. Strong solar radiation combined with low temperature shortly after snowmelt is potentially damaging, and therefore anthocyanins are synthesized in leaves as a photoprotective mechanism (Oberbauer and Starr 2002, Steyn et al. 2002, Close and Beadle 2003). Thus, high levels of anthocyanins in early growing season is considered an important protective mechanism (Oberbauer and Starr 2002, Mac Arthur and Malthus 2012), and our monitoring shows that flavonoids in new leaves increased during the first few weeks of the growing season. Similar anthocyanin coloration in *V. myrtillus* during an unusually cool summer with multiple frost events has previously been reported (Bjerke et al. 2014).

Petrova (2015) hypothesizes that facultative wintergreenness of Apiaceae species may be a recapitulation from evergreen ancestors. This is also a likely hypothesis for the observed wintergreenness of *V. myrtillus*, as the genus *Vaccinium* consists of both evergreen and deciduous species. *Vaccinium myrtillus* is, in fact, known to hybridize with the evergreen *V. vitis-idaea*. The hybrid is known as *V.* × *intermedium* Ruthe. It is winter- or evergreen, and its leaf and stem morphology is intermediate between the two parent species (Ritchie 1955, Ponikierska et al. 2004). This hybrid differs from our study plants in several morphological characters and by always overwintering with leaves attached. There are no indications that our study plants are of hybrid nature, because in all other characters, the plants were morphologically and phenologically identical to *V. myrtillus*. We therefore think that overwintering of secondary leaves is a widespread but overlooked feature in this species, and in fact, we had seen this once previously, in a northern Swedish population.

This study also shows that the optical chlorophyll meter is a useful tool for monitoring the physiological status of wild, boreal plants. This instrument was primarily developed for commercially grown crop plants with large leaves (Cartelat et al. 2005, and manufacturer's information available at www.force-a.com). The major challenge with *V. myrtillus* and other boreal or arctic plants is their small leaf sizes. Firstly, it is challenging to place the leaves directly inside the measuring circle of the sensor. Secondly, it is challenging to find leaves that are large enough to cover the entire measuring circle. As readings are area-based, the entire circle should be covered. By opening the measuring head gently and visually checking the measuring circle from a skewed angle (not possible to check from a perpendicular view), we were able to state whether the entire measuring circle was covered or not. If not entirely covered, the readings were discarded. There is always a risk that the leaf moves out of position during opening of the measuring head, and in such cases, the readings should also be discarded. The strong correlation between chlorophyll content and leaf colour state show that it is possible to monitor health and state changes over time in this small-leaved plant. We found a close correlation between chlorophyll concentrations and the nitrogen index NBI in both overwintering and new leaves. This was as expected, since the photosynthetic capacity of leaves is related to the nitrogen content primarily because the proteins of the Calvin cycle and thylakoids represent the majority of leaf nitrogen (Evans 1989).

Since we monitored the plants only with the Dualex meter, we cannot state the exact contribution of the wintergreen leaves to the plants' carbon budget in the preceding growing season. *Vaccinium myrtillus* is a clonal plant with a large root system, hence, much carbon is stored belowground (Grime et al. 1988). However, two consecutive summers with near-complete leaf defoliation must have resulted in a considerable decline in the plants' carbon stocks, as shown from other but similar habitat types (Bokhorst et al. 2015, Parker et al. 2017). We therefore think the carbon sequestration of the wintergreen leaves helped the plants in the critical first phase until new side branches with new leaves were developed. It might be that other boreal plants respond similarly to insect herbivory or other stress-induced damage. Facultative wintergreenness may therefore be a strategy in other boreal species. However, to assess this, it is highly necessary to study plants both in autumn until they become covered in snow, and in spring, from snowmelt and onwards. A reason why this has not been detected previously in *V. myrtillus* may be because field studies generally start several weeks after snowmelt, as was the case in the study by Martz et al. (2010). In such situations overwintering leaves may be misinterpreted as newly emerged leaves.

Following larval-induced leaf defoliation, we have also observed green, secondary leaves on birch (*Betula pubescens*) and rowan (*Sorbus aucuparia*) trees in October after the first snow of the season (unpubl.). However, we have never seen green leaves on these trees in spring. Overwintering of photosynthetic tissues above the snowpack is much more stressful than overwintering underneath it (Bokhorst et al. 2016), and therefore, secondary leaves on trees other than conifers have low probability of surviving until next spring under typical boreal winter conditions.

To conclude, here we have reported on a hitherto little-known phenotypic plastic response in the widespread boreal plant *V. myrtillus* following stress events. We show that this normally deciduous plant is facultatively wintergreen after growing-season leaf defoliation. We have also previously observed a similar attempt of leaf overwintering in this species (Fig. 1c) following experimentally induced stress (Bokhorst et al. 2008). The occasional overwintering of basal leaves in *V. myrtillus*, as reported by Grime et al. (1988), may represent a similar case of stress, or these leaves may be developed naturally late in the growing season and are therefore capable of overwintering. The phenotypic plasticity of this species may play a key role in its success, as shown by its wide Eurasian boreal–alpine distribution and abundance.

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